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AUTHOR(S):

IWANO, Taizo

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NOCTURNAL ACTIVITY OF A CAPTIVE AYE-AYE (*Daubentonia madagascariensis*)

Taizo IWANO
Department of Zoology, Faculty of Science, Kyoto University

ABSTRACT This report aims to clarify the nocturnal activity of the aye-aye (*Daubentonia madagascariensis*) under captive conditions to compare it with that under natural conditions.

The aye-aye was nocturnal and showed activity at any time at night. However, from 02:00 hrs until just prior to dawn, it often rested. It frequently returned to the nest throughout this period to take long rests of more than half an hour.

The aye-aye's activities were classified into four categories: feeding, moving, resting and other activities. The average proportions of these activities were 14.8%, 25.3%, 56.7% and 3.2%, respectively. The relative proportions of the activities showed seasonal changes. Rises in atmospheric temperature were highly correlated with increases in the proportion of moving ($r=0.908$). Generally speaking, the proportion of feeding was high in the early evening and gradually fell as night progressed.

The four activities were sub-divided into several component acts. In terms of component acts, hanging was positively correlated with a rise in temperature ($r=0.889$), while sitting was negatively correlated ($r=-0.862$), suggesting that the activity of the aye-aye is generally enhanced with rises in atmospheric temperature.

The aye-aye engaged in tapping and gnawing throughout the period. These acts consisted of a long duration of gnawing at definite places on the window or the steel frame of the door.

Since the proportion of feeding activity was virtually undetermined under natural conditions because of intermittent observations and fragmented data, we assumed that it would be similar to that seen in the captive condition. On average, the aye-aye engaged in feeding for 89 minutes during a night, and consumed 48.5 ramy fruits or ingested 212 kcal. The energy intake from this quantity of ramy fruits would be sufficient, considering the basal metabolic rate of prosimians. These analyses support a hard-nut adaptation hypothesis suggesting that ramy fruit is an important staple food of the aye-aye.

During the period of study, the aye-aye was presented with 12 diet items such as coconuts, ramy nuts, bread, etc. The weight of food consumed during meals was measured over 16 nights to calculate the energy intake of the aye-aye, which was found on average 306.1 kcal per meal.

The response of the aye-aye to light was markedly different from other nocturnal prosimians. The aye-aye was not apparently disturbed when exposed to intense light.

Key Words: *Daubentonia madagascariensis*; Aye-aye; Nocturnal activity; Food; Feeding behavior; Energy intake; Hard-nut adaptation hypothesis.

INTRODUCTION

Since its discovery in the 18th century, a small number of aye-ayes has been kept

privately as well as in public facilities such as zoos (Bartlett, 1862; Owen, 1863; Millot, 1952; Petter et al., 1977). However, no quantitative, long-term surveys on the nocturnal activity of aye-ayes in captivity or in the wild have ever been conducted. Recently, Winn (1989) started a study at the Paris Zoological Garden on three individuals which had been captured on the east coast of Madagascar in 1986 (Albignac, 1986), and reported a number of important observations, especially regarding mother-infant relationships. Despite such recent trends, until now, no quantitative study has been presented on the nocturnal activity of aye-ayes.

Through observation of wild aye-ayes at Nosy Mangabe, I gained some insights into the aye-ayes' daily activities, such as feeding (Iwano, 1991a). However, the result was far from complete in disclosing the nocturnal activity of aye-ayes, owing to my inability to follow the aye-ayes' activities in the dark for a considerable portion of the observation time. Our experience indicates that difficulties in the direct observation of aye-aye behavior are due to the following factors: the aye-aye's activity is nearly completely nocturnal, it usually moves through the crown of tropical rain forests, it moves apart from other conspecifics, it rarely vocalizes, and it often hides in thickets when resting.

This investigation was carried out at, and under the auspice of, the Botanical and Zoological Park of Tsimbazaza (Tsimbazaza Zoo), Madagascar Democratic Republic. The aim of the study was to elucidate the nocturnal activity of one adult female aye-aye housed at the park.

I focused on the feeding habits of the aye-aye in an effort to explain preferences toward certain diets in terms of their energy content, and to determine the degree to which the food preference of the aye-aye is related to its specialized morphological traits.

The activity of a captive aye-aye will, of course, be more or less different from that in the wild, but the study of its nocturnal activity should contribute in gaining further insights into the ecology of the aye-aye at large.

STUDY SITE AND METHODS

I. Study Site

Antananarivo, the capital of Madagascar (1,381 m above sea level and 18°56'S), is situated in the highland area of the central part of Madagascar. Its temperature averages 17.3°C annually. In terms of monthly average temperature, July is the lowest (13.3°C) and January is the highest (20.1°C). The difference between the highest and lowest temperatures within a day ranges from 6°C to 16°C (Donque & Petit, 1967; Donque, 1972).

The annual precipitation at Antananarivo is 1,354 mm or half that of the forested regions along the east coast, such as Maroantsetra. The average monthly precipitation is highest in January (309 mm) and lowest in July (7 mm) (Donque & Petit, 1967).

II. Methods

The aye-aye under study, an adult female, was one that had been housed since 1988 at the Tsimbazaza Zoo, Antananarivo. It was reported that this animal had been captured by some local inhabitant near Antsohihy on the west coast of Madagascar and was then protected by a press agent who later donated it to the zoo.

Plate 1. A picture of feeding facility of the aye-aye.

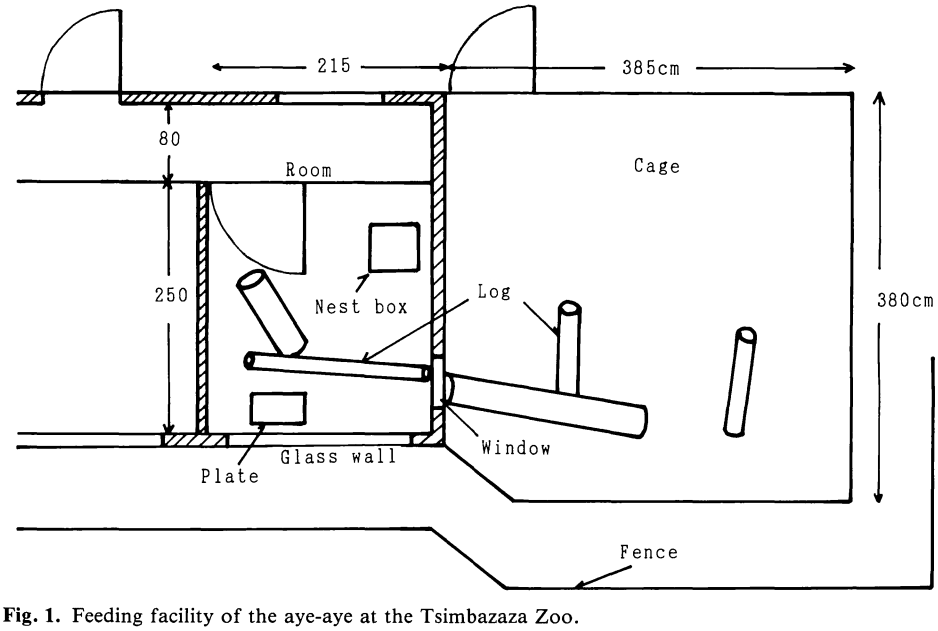

Fig. 1. Feeding facility of the aye-aye at the Tsimbazaza Zoo.

The animal was housed in a two-compartment feeding facility consisting of a cage (14.6 m^2) whose ceiling and sides were covered with iron mesh, and a feeding room (5.4 m^2) which was equipped with a nest box and fitted with a front glass panel (Plate 1, Fig. 1). Food was placed on the floor of the feeding room, and the aye-aye came out of the nest box at night and consumed the food. Food was given once-a-day between 4 to 5 o'clock in the evening, and the quantity was sufficient to meet the appetite of the aye-aye, as was evidenced by the fact that the aye-aye always left the portion behind. Unconsumed food was removed the next morning.

The study period was 35 nights between June and November 1989. The total observation time was 371 hours, or 43,375 30-sec samples based on the instantaneous observation method (or 43,369, in terms of instances of observation) (Table 1). In addition, as a part of another series of studies, I measured the consumed weight of individual meals for 16 nights between September and November, to calculate their respective energy values.

1. Observation of the Aye-aye's Activities Based on the Instantaneous Method

The aye-aye's activities was observed over half a year from winter to summer. Although this cannot provide sufficient data to obtain a full understanding of annual changes in the aye-aye's activities, it allows me to gain insights into their seasonal habits. The results regarding the manipulation of the aye-aye's digits are to be presented elsewhere (Iwano, 1991b).

Observations were carried out from 6:00 hrs in the evening until 4:59 hrs the next morning. Observations prior to and following that interval were excluded from the study, because the aye-aye was virtually inactive.

The aye-aye was active at 4:00 hrs in the evening in May (Mr. Rakotoarisoa; the curator of Tsimbazaza Zoo, personal communication). Along the west coast of Madagascar, aye-ayes are occasionally active during daylight hours in October (Mr. H. Fukazawa, personal communication). Thus, it is likely that aye-ayes occasionally become active when it is still light. Even admitting such activity, however, I think the observation period totaling 11 hours between 18:00 and 5:00 covers a major part of the aye-aye's activity.

In accordance with the instantaneous sampling method (Altmann, 1974), I considered the aye-aye's activities in terms of units, each of 30 second duration, and recorded the location of the aye-aye and the type of activity for each unit. Such observation units will be referred to as samples here after. Although this method does not always allow one to sample all brief activities, principal activities determining the aye-aye's activity pattern, such as sleeping and feeding, owing to their

Table 1. Study period and observation samples on the activity of a captive aye-aye (*Daubentonia madagascariensis*) at the Tsimbazaza Zoo in 1989.

	June/July	August	September	October	November	Total
Days	7	6	6	7	9	35
Hours	72	63	65	74	97	371
Hours/Day	10.3	10.5	10.8	10.6	10.8	10.6
Samples	8,395	7,335	7,617	8,736	11,292	43,375
Samples/Day	1,199.3	1,222.5	1,269.5	1,248.0	1,254.7	1,239.3

comparatively long duration, could be fully covered with this method.

The aye-aye's activities were defined in terms of place and type.

(1). Gross categories of place of activity

There were two areas where a given activity of the aye-aye occurred: the cage and the feeding room. The activity site was divided into minor categories: within the cage, sub-categories included "on the ground," "on tree branches," and "on wire mesh." (The sides and ceiling of the cage were fitted with mesh on which the aye-aye often climbed or clung). In the feeding room, the place of activity was subdivided into the following minor categories: "on the ground," "on tree branches," "on wire mesh" (the feeding room also had wire mesh on the wall facing the aisle), "in the nest box," "on the roof of the nest box," "under the nest box," "behind the leaves" (a tree branch covered in leaves dense enough to hide the aye-aye's body was placed in front of the nest box), and "on the window" (which was installed as a passage way on the wall dividing the feeding room and cage).

(2). Gross categories of activities

The aye-aye's activities were roughly divided into four categories: feeding, resting, moving and other activities. These four general activity categories were further subdivided into elementary acts as follows:

Feeding was subdivided into eating and drinking. When the aye-aye was given a coconut, it ate the pulp and drank the milk simultaneously. The two acts were so inseparable that they were classified under the same feeding category.

Moving was subdivided into walking, climbing, hanging and jumping.

Resting was subdivided into standing, sitting, sleeping, self-grooming, and suspending. Suspending differs from common hanging in that the animal is motionless for a span of at least 30 seconds, whereas in common hanging, the animal is moving. Sleeping can be distinguished from sitting. For example, when the animal takes a rest on the ceiling of the nest box, it crouches, coils its tail on its ventral aspect, and directs its head inward. The aye-aye sits with its rump on the floor and remains motionless. Coiling the tail inward under the body is a characteristic posture indicating the animal is in a relaxed state. Entry into the nest box was also interpreted as sleeping, although I could not determine exactly what activity the animal was engaged in.

Other activities include a variety of elementary and complex acts, such as excreting urine and feces; gnawing at trees, window-frames and the steel parts of the door; tapping something with the finger tips; smelling; licking something other than foods; holding something including foods; pulling tree branches outside the nest box from inside the nest box; and playing. Playing is a compound activity including a number of elementary acts, and consists of various brief actions such as running with something in the mouth, tumbling about on the floor, lying on the back on the floor, etc. However, I feel it is more reasonable to consider a series of play acts as one whole. Thus, such actions were classified as a whole under the same category of playing.

To facilitate observation, torch light was shone directly upon the aye-aye, which was apparently not disturbed by such artificial intervention. Moreover, for close observation, I often approached within 20 cm of the aye-aye, with the glass panel between us, but the animal remained unresponsive to such intrusion. This

characteristic indifference of the aye-aye toward external changes was further demonstrated by its behavior during video recording: Two lights, 150 thousand lux each, were shone onto the animal from about 2 m, but this much illumination did not appear to have the slightest effect on its behavior, and the animal even ate food, facing the light. Thus, light and the presence of humans in close proximity had practically no effect on the animal. However, the animal apparently paid attention to signs and sounds of human presence behind the door of the feeding room opposite the glass panel, and sometimes even fled beneath the nest box.

2. Measurement of Food Intake

For 16 nights between September and November 1989, I measured food intake. Using a platform scale, I weighed foods that were given to the animal and the unconsumed remains. Food intake was obtained by subtracting the latter from the former. The total energy intake was calculated from the food intake data.

3. Data Analysis

Observation of the aye-aye's nightly activities was analyzed by the hour under the following categories: place of activity, type of activity, kind of acts constituting each activity, and feeding behavior on individual food items. For each categories, the relevant samples were summed and their proportion relative to the gross total (%) was calculated.

The aye-aye's activity varied from night to night: one evening, the animal would start eating as soon as it awoke and exited from the nest box; another night, it would take a long rest after coming out of the nest box; and still another night, it would move around before sitting down to eat. This variety was reflected in the records of the aye-aye's nightly activity, where the proportion of each activity varied considerably from night to night.

To obtain a general pattern of the aye-aye's nightly activity, the data were analyzed for each month, and the monthly data thus obtained were compared. More detailed analyses involved the examination of hourly changes in individual activities and the average single duration of principal acts constituting an activity. All of these data were inspected to determine seasonal patterns in activities and their component acts. Nutritional approaches to food intake of the aye-aye were treated as a separate subject.

RESULTS

I. Seasonal Change in Activity Pattern as Analyzed from Its Component Acts

The data of the aye-aye's nightly activity were summed for each month from August to November (Table 2). For each month, samples of a given activity were summed, and the total was expressed as a percentage of the gross total. Then, the relative distribution of individual activities were compared for different months. For June and July, however, the data were combined together. Two samples each in July, August and September (six in total) could not be ascribed to any definite activity category, but observation records were taken. Thus, the total number of ac-

Table 2. Activity of the aye-aye in the Tsimbazaza Zoo between June and November, 1989 (Observation samples).

	Month	June-July	August	September	October	November	Total
	Hour	72	63	65	74	97	371
	Sample Number	8,395	7,335	7,617	8,736	11,292	43,375
Place	Room	7,098	6,332	5,893	6,338	6,276	31,937
	Cage	1,297	1,003	1,724	2,398	5,016	11,438
Point	R. Ground	1,719	1,279	1,329	1,026	669	6,022
	C. Ground	494	317	244	301	693	2,049
	R. Tree	469	190	252	425	495	1,831
	C. Tree	240	290	576	879	1,993	3,978
	On Nest	1,221	1,124	934	431	1,133	4,843
	Under Nest	234	22	241	0	23	520
	In Nest	3,450	3,527	2,923	4,274	3,745	17,919
	R. Wire Net	76	66	73	12	25	252
	C. Wire Net	439	385	904	1,214	2,330	5,272
	R. Window	53	135	141	174	186	689
Activity	Feeding	1,522	1,080	1,258	1,270	1,300	6,430
	Moving	1,678	1,290	1,852	2,193	3,940	10,953
	Resting	5,002	4,774	4,286	5,061	5,463	24,586
	Other	191	189	219	212	589	1,400
	Total	8,393	7,333	7,615	8,736	11,292	43,369
Behavior	Eating	1,456	1,044	1,223	1,210	1,260	6,193
	Drinking	66	36	35	60	40	237
	Walking	1,109	911	952	1,059	1,898	5,929
	Climbing	178	19	2	66	238	503
	Hanging	279	332	873	970	1,639	4,093
	Jumping	112	29	25	115	165	446
	Standing	17	78	37	137	618	887
	Sitting	791	934	783	608	725	3,841
	Self-grooming	308	164	120	55	307	954
	Sleeping	3,886	3,592	3,299	4,216	3,708	18,701
	Suspending	0	6	47	25	100	178
	Rest. Unknown	0	0	0	0	5	5
	Tapping	39	54	36	43	158	330
	Excretion	28	32	20	22	25	127
	Gnawing	112	97	127	121	270	727
	Smelling	7	5	15	4	12	43
	Licking	5	0	21	3	23	52
	Holding	0	0	0	2	0	2
	Pulling	0	0	0	20	91	111
	Playing	0	0	0	0	10	10
	Average Temperature (°C)	13.3	13.6	15.0	17.9	19.3	

Six activity samples are unavailable.
C.: Cage; R.: Room.

tivity samples (43,369) is six units less than the total number of observation samples (43,375).

1. Resting

The proportion of resting was predominant among individual activities

throughout the months studied. Resting was followed by moving, feeding, and other activities, in that order. The high proportion of resting can be explained by the fact that the aye-aye often entered the nest box to take rests lasting 30 minutes to one hour.

The longest total duration of resting ever observed in my study was seven hours on August 11 to 12 (which included a span of five hours from 0:00 to 4:59 hrs), and the proportion of resting on that day was 90.7%, the highest of all the resting proportions. Observation records for October 16 to 17 showed a continuous rest of four hours, with brief stretches of resting occurring frequently throughout the observation period, thus resulting in a high resting proportion of 85.1%. The same tendency was observed on August 13 to 14 when the proportion of total resting was 72%, with the longest continuous rest lasting five hours from 21:00 to 1:59 hrs. Observation periods in which the total duration of resting exceeded three hours occurred on nine nights.

Thus, owing to the aye-aye's predilection to rest for long continuous periods as well as brief and frequent intervals, the predominant relative monthly activity of the aye-aye was resting. Resting accounted for more than 50% of monthly activities except in November. The resting proportion was compared for different months, and significant differences were found (test of the difference between two proportions, $p<0.05$), except for the following: June/July and November, and September and November.

2. Seasonal Change in Activity Proportions (Fig. 2)

The relative distribution of individual activities showed seasonal (or monthly) changes. The proportion of "other activities," however, did not show such seasonal changes: It remained virtually invariable from June to October, except in November when the proportion was significantly different from that in other months.

The monthly proportion of feeding showed a falling tendency from 18% in June/July to 11% in November with, however, no significant difference between August and October (test of the difference between two proportions, $p>0.05$).

The most conspicuous seasonal change was in the proportion of moving. The moving proportion in June/July was nearly equal to the corresponding feeding proportion, whereas in November, it rose to three times that of the corresponding feeding proportion. The ratios between the moving and feeding proportions were significantly different for all months compared (test of the difference between two proportions, $p<0.05$), except for between September and October.

The proportion of "other activities" in November was significantly higher than that in any other month (test of the difference between two proportions, $p<0.01$). This difference was due to the fact that tapping and gnawing, two principal components of "other activities," increased in November.

3. Seasonal Change in Individual Acts

The principal acts constituting moving are walking and hanging. Hanging rose from 3.3% in June/July to 14.5% in November. In contrast, walking did not show any noticeable change through the months studied, except in November (test

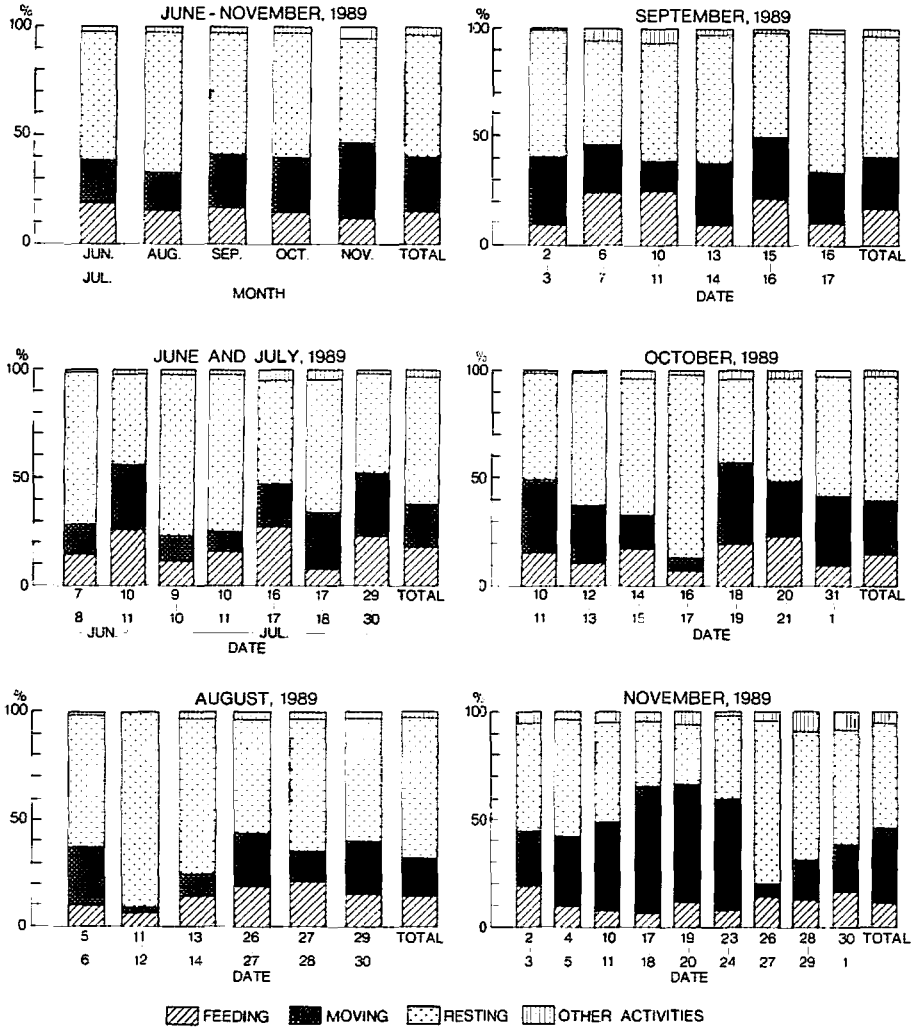

Fig. 2. Percentages of four activities for each night and month for the aye-aye at the Tsimbazaza Zoo in 1989.

of the difference between two proportions, $p > 0.05$).

The seasonal changes in activity were reflected in the changes in the use of place. Use of wire mesh increased from 5.2% in June/July to 20.6% in November. The use of tree branches also increased from 2.9% in June/July to 17.6% in November. In summary, the aye-aye was active outdoors in November and especially preferred to move along tree branches or hang from wire mesh.

Elementary acts that constituted resting included sitting, self-grooming and sleeping, and their monthly proportions were found to differ significantly from month to month (test of the difference between two proportions, $p < 0.05$).

Among the elementary acts involved in "other activities," tapping and gnawing showed a characteristic seasonal change: their monthly proportion was high only in November. On the other hand, excreting remained constant throughout all months studied.

In November, the aye-aye tended to display unusual behaviors and diversified activities. Unusual activities included a series of playful actions, such as rolling about on the floor, jumping holding something in the mouth, or a combination of such actions. The frequency of gnawing and tapping increased as well, as previously noted.

"Pulling," or pulling twigs into the nest box, was initially observed in October, and its proportion increased in November. This act may be related to nest building for breeding, but nest-building did not actually ensue.

4. Relation of the Activities to the Temperature

Feeding showed a gradual decrease from June/July to November (the decrease leveled off between August and October), while the proportion of moving gradually rose (the lowest level was reached in August). A parallel tendency was observed in the monthly change in atmospheric temperature in the region. When the monthly change in individual activities was compared with that of the average monthly temperature at Antananarivo (see Table 2), only the moving proportion was found to show a significant positive correlation ($r=0.908$, $p<0.05$).

Among the component acts constituting moving activities, the hanging proportion showed a positive correlation ($r=0.889$, $p<0.05$), while among resting activities, the sitting proportion was negatively correlated with temperature ($r=-0.862$, $p<0.05$). The walking proportion was unrelated to temperature ($r=0.608$, $p>0.05$).

Obviously, not all of the aye-aye's activities can be explained simply by temperature changes in its environment. However, the study period corresponded with a transition from winter to summer and the large temperature change may have affected the aye-aye's behavior through changes in environmental factors. It is noteworthy that the aye-aye was more inclined to move by hanging from the wire mesh as the temperature rose, a feat requiring a considerable energy expenditure. At night, when the aye-aye was generally active, sleeping, a component of resting, appeared to be unaffected by temperature changes. Sitting, another component of resting, decreased with rises in temperature. This suggests that the aye-aye is more active in summer than in winter.

II. Relative Distribution of Individual Activities and Their Respective Component Acts by Hour

The aye-aye's activity showed wide variation when analyzed by hour. The animal sometimes started feeding soon after sunset, while at other times, it was rather reluctant to feed and did not start feeding until 20:00 hrs.

The aye-aye's activity varied so widely from night to night. Nevertheless, when the aye-aye's activities are summed by hour and month, more or less consistent tendencies emerge. Generally speaking, the aye-aye spent most of the time resting

between 3:00 and 4:00 hrs. Feeding was high early night, and gradually fell toward late at night. This pattern was common to all the months studied (Fig. 3).

Feeding, moving and "other activities" were combined as representing restlessness or "positive" activity of the aye-aye, and the proportional sum of the activities was calculated for each month. The proportion of positive activity was low, less than 50%, from June/July to August. In contrast, the proportion of positive activity was high from September to November. In these months, however, the individual activities constituting positive activity were different from each other.

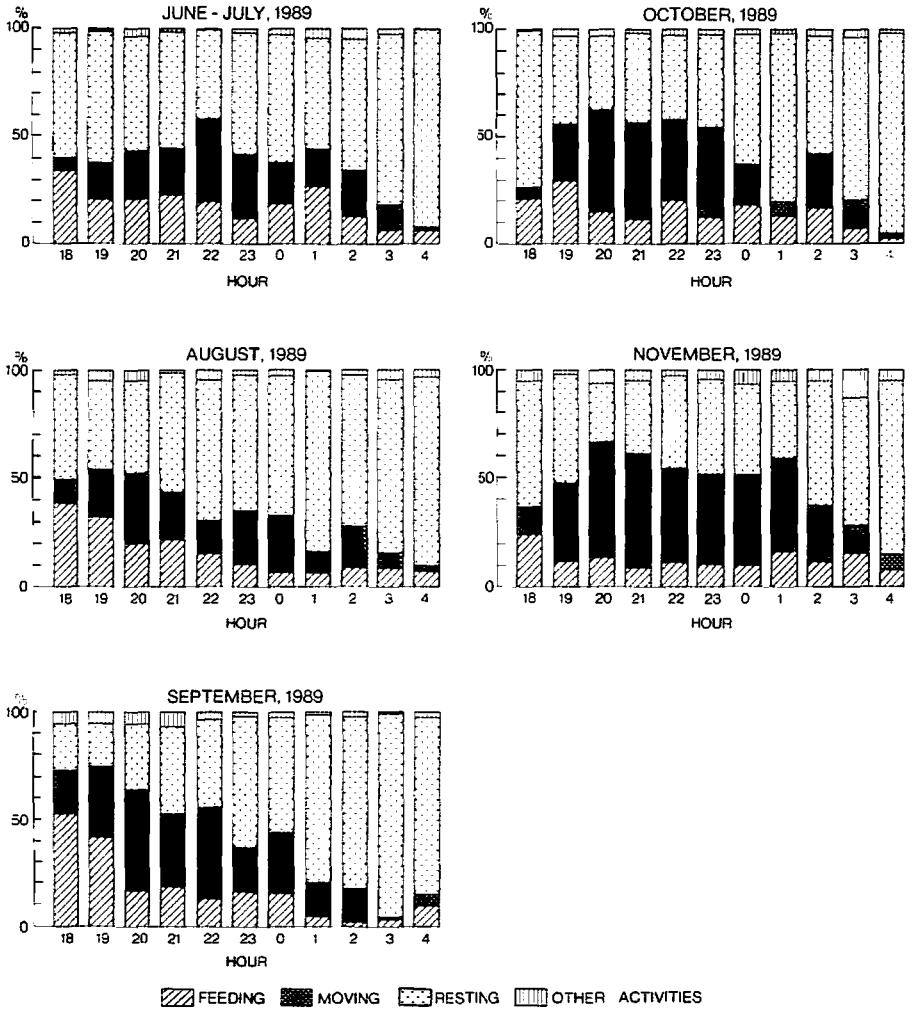

Fig. 3. Hourly patterns of feeding, moving, resting and other activities during the night for the aye-aye at the Tsimbazaza Zoo in 1989.

III. Duration of Individual Component Acts

In this paper, duration refers to the number of continuous samples recorded. Although acts consisting of a series of brief movements, such as tapping, the duration may be less than ten seconds, I can calculate such duration with the instantaneous sampling method, if such acts were repeated frequently.

The aye-aye often took long rests during the night. When the animal entered the nest box, it habitually took rests lasting longer than 30 minutes and sometimes all through the early hours of the next morning. Similarly for moving, there were often instances exceeding 30 minutes in duration. Such long durations were not seen for other component acts.

I could easily determine seasonal changes in the duration of component acts. However, for resting and moving, the results were the same whether analyzed in terms of hourly proportion or their exact duration. Here, I analyzed seasonal changes in the duration of other component acts, such as eating, drinking, self-grooming, tapping and gnawing, which have comparatively short durations. The average was calculated for each month and compared (Table 3).

1. Eating

The average eating bout was longest in June/July and the briefest in August. The longest bout occurred at zero to one hrs on June 11 (102 sample lengths for eating an egg). The average eating bout became relatively short after August, but did not show significant reduction thereafter.

2. Drinking

The longest drinking bout was 14 sample lengths at 0:00 hrs on June 8. The monthly average was relatively high in June/July and November, but low from August to October. What this pattern means remains unclear.

3. Self-Grooming

Table 3. Average bout of eating, drinking, self-grooming, tapping and gnawing by the aye-aye between June and November, 1989.

Month		Eating	Drinking	Self-Grooming	Tapping	Gnawing
June-July	Ave.	10.55	5.50	2.68	1.39	2.55
	s.d.	12.30	4.37	3.43	0.82	1.88
August	Ave.	5.47	1.33	1.78	1.93	1.59
	s.d.	5.71	0.54	1.69	1.46	1.32
September	Ave.	6.27	1.40	2.73	1.50	2.08
	s.d.	5.79	0.80	3.99	0.65	1.88
October	Ave.	7.64	1.94	1.96	1.34	2.27
	s.d.	6.56	0.98	2.87	0.69	1.03
November	Ave.	6.89	2.22	1.88	2.14	1.89
	s.d.	6.62	0.79	1.68	1.67	1.37
Total	Ave.	7.36	2.21	2.21	1.66	2.08
	s.d.	1.95	0.46	0.46	0.42	0.33

Unit: 30 second interval samples.

The longest self-grooming bout was 29 sample lengths (at 0:00 to 1:59 hrs on July 17). The proportion was high in June/July and November, and low from August to October. However, the monthly averages did not show comparable patterns of seasonal change, although significant differences were observed among the months studied.

4. Tapping

The average bout of tapping was significantly longer in November than in any other month studied. This coincides with the increased proportion of self-grooming for this period.

5. Gnawing

Monthly changes in the average duration for gnawing were not clear as for tapping. The average was constant regardless of the season. This act, once initiated, continued for a certain stretch of time without interruption, in contrast to tapping.

IV. Diet

1. Food Items and Their Relative Intake

A total of 12 different food items, excluding coconut water, were given to the aye-aye during the observation period (Table 4). Coconuts, bread, bananas, tomatoes, sugar cane and papayas were each served in an amount sufficient to meet the appetite of the aye-aye, so that a portion was always left unconsumed the next morning. The following food items were not given in sufficient amounts: Eggs were usually served one per meal, and the yolk was completely consumed while the white was uneaten. If more than two eggs were served, more yolk would have been consumed by the aye-aye. This also held true for ramy and honey. These foods were usually consumed completely. I assume that amounts larger than provided would also have been consumed.

At the Tsimbazaza Zoo, the aye-aye is given a variety of foods to maintain a good nutritional balance. Thus, the aye-aye was served three to seven different food items every night. Of all the food items served, the aye-aye spent the longest time (or the longest proportion of eating time) on coconut, followed by ramy fruits, bread, bananas, etc. Coconut was the food item which was most easily obtainable during the observation period, and was most amply served.

Comparison of sample lengths of coconut consumption to the sample lengths of all other food consumption (the relative coconut eating duration) revealed seasonal changes in coconut consumption, with some decrease as temperature increased ($r=-0.837$, $p<0.05$).

Ramy nuts (*Canarium madagascariense*) were picked from trees planted on the grounds of the Tsimbazaza Zoo, and were served to the aye-aye from August, when the trees bear fruits, until November. The amount of ramy fruits given to the aye-aye was comparable to other food items. Proportional feeding on ramy was lowest in August, and leveled off from September to November.

Bread was often served soaked in sweetened condensed milk, and was consumed avidly by the aye-aye. It was given as a staple food to the aye-aye. In contrast

Table 4. Seasonal changes of food composition for the aye-aye in the Tsimbazaza Zoo between July and November, 1989.

Food	Month					Total
	July	August	September	October	November	
Coconut	627	446	421	367	236	2,097
	(67.9)	(41.3)	(33.5)	(28.9)	(18.2)	(36.0)
Ramy	—	162	307	284	285	1,038
	—	(15.0)	(24.4)	(22.4)	(21.9)	(17.8)
Bread	53	113	207	230	333	936
	(5.7)	(10.5)	(16.5)	(18.1)	(25.6)	(16.0)
Banana	49	211	186	27	—	473
	(5.3)	(19.5)	(14.8)	(2.1)	—	(8.1)
Honey	—	—	61	170	147	378
	—	—	(4.8)	(13.4)	(11.3)	(6.5)
Egg	15	55	30	44	160	304
	(1.6)	(5.1)	(2.4)	(3.5)	(12.3)	(5.2)
Tomato	—	38	11	64	48	161
	—	(3.5)	(0.9)	(5.0)	(3.7)	(2.8)
Sugar cane	124	—	2	23	—	149
	(13.4)	—	(0.2)	(1.8)	—	(2.6)
Papaya	21	11	2	—	26	60
	(2.3)	(1.0)	(0.2)	—	(2.0)	(1.0)
Palm fruit	—	—	—	—	25	25
	—	—	—	—	(1.9)	(0.4)
Milk	—	1	6	—	—	7
	—	(0.1)	(0.5)	—	—	(0.1)
Pineapple	—	—	2	—	—	2
	—	—	(0.2)	—	—	(0.0)
Coconut water	1	34	23	47	30	135
	(0.1)	(3.1)	(1.8)	(3.7)	(2.3)	(2.3)
Water	—	—	—	13	10	23
	—	—	—	(1.0)	(0.8)	(0.4)
Unidentified	34	9	—	1	—	44
	(3.7)	(0.8)	—	(0.1)	—	(0.8)
Total	924	1,080	1,258	1,270	1,300	5,832
	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)

—: In these months, these foods were not fed.
Upper: number of samples; Lower: percentages.

with coconut, it was more avidly consumed with the rise in temperature ($r=0.934$, $p<0.05$). How a rise in temperature can affect the appetite of the aye-aye toward bread remains unclear.

Bananas were so avidly consumed by the aye-aye that in August, the feeding time on bananas was longer than on ramy fruits or on bread. After October, however, the proportional feeding time on bananas rapidly decreased. This phenomenon may possibly be related to changes in preference toward bananas (or their status as a food), as seen for coconuts.

Usually, one egg was given per a meal. The small amount of the egg probably explains why the proportional feeding time for eggs was low compared to that for other food items. The skill with which the aye-aye consumes an egg demonstrates that the animal is well adapted to this food item.

Passion fruits and oranges were also presented to the aye-aye, but they were not eaten. In addition, the animal did not eat the leaves of tree-branches that were always placed in the feeding room to serve as nest material.

Table 5. Weights and energies of foods eaten by the aye-aye in the Tsimbazaza Zoo between September and November, 1989.

Date	Food items												Total energy (kcal)
	CO.	RA.	BR.	BA.	HO.	EGG.	TO.	SU.	PA.	AV.	MA.	C.W.	
Sep. 16	40	—	10	35	+	20	—	—	—	—	—	—	
	136		31	31	+	74							272
Oct. 24	50	—	30	10	50	—	65	—	—	—	—	—	
	170		93	9	147		10						429
25	10	—	30	30	—	35	—	—	—	—	—	—	
	34		93	26		82							235
26	10	—	30	—	27	35	20	—	—	—	—	—	
	34		93		79	82	3						291
27	—	—	40	—	—	30	—	—	—	10	10	75	
			124			75				30	7	11	247
28	—	—	35	—	36	—	80	—	50	—	—	—	
			109		106		13		25				253
29	—	5	30	30	—	10	10	—	50	—	—	—	
		31	93	26		37	2		25				214
30	—	—	30	—	36	—	60	—	60	—	—	—	
			93		106		10		29				238
31	—	—	50	—	—	10	10	30	—	—	—	—	
			155			37	2	78					272
Nov. 1	—	—	30	—	36	—	—	—	—	—	—	—	
			93		106								199
2	20	14	40	—	—	20	—	—	—	—	—	140	
	68	83	124			74						20	369
3	20	—	20	—	60	—	10	—	30	—	—	—	
	68		62		176		2		15				323
4	20	—	150	—	—	20	—	—	—	—	—	—	
	68		465			74							607
5	10	—	30	—	36	—	40	—	—	—	—	—	
	34		93		106		6						239
6	30	—	50	—	60	—	50	—	—	—	—	—	
	102		155		176		8						441
9	20	5	40	—	—	—	—	—	80	—	—	100	
	68	26	124						39			14	271

Upper values: weight (g); Lower values: energy (kcal).
+: food given but not eaten; —: food not given.
Abbreviation of food items, latin names and their energies (kcal/100 g).

CO.	Cocount	(*Cocos nucifera* L.)	340
RA.	Ramy	(*Cananium madagascariense* Engle.)	584
BR.	Bread with milk		310
BA.	Banana	(*Musa sapientum* L.)	87
HO.	Honey		294
EGG.	Egg		372
TO.	Tomato	(*Lycopersicum esculentum* Mill.)	16
SU.	Sugar cane	(*Saccharum officinarum* L.)	259
PA.	Papaya	(*Carica papaya* L.)	49
AV.	Avocado	(*Persea americana* Mill.)	191
MA.	Mango	(*Mangifera indica* L.)	68
C.W.	Coconut water		14

2. Estimation of Energy Intake

The energy intake was calculated from the the ingested amount of foods (Table 5). The energy intake averaged 306.1 kcal per meal (range=198.8–607.4, S.D.=107.46, n=16).

DISCUSSION

I. Nocturnal Activity

Studies on the nocturnal activity of the aye-aye are very limited in number (Petter & Petter-Rousseaux, 1959; Petter, 1962; Winn, 1989). Furthermore, results based on quantitative measurement have never been presented. The present investigation can thus be viewed as a first step toward elucidation of the activity of the aye-aye. However, this investigation suffers from a number of limitations: the study period was short, and depended upon a single adult female aye-aye, secluded in a narrow space that permitted only limited movement and feeding on a routine food menu.

Our major findings on the nocturnal activity of the aye-aye are as follows.

The aye-aye was nocturnal and active at all times at night, but, from 2:00 hrs in the morning until just prior to dawn, it often took a rest. In addition, it returned to the nest to take long rests of more than half an hour. Resting comprised 56.7 percent of its nocturnal activity. Such proportions of the activities showed seasonal changes. Rises in atmospheric temperature were highly correlated with increases in the proportion of moving and hanging. Generally speaking, there was more feeding early in the night than later. The aye-aye was observed to engage in tapping and gnawing on all nights during the study period. It gnawed at definite places on the window or the steel frame of the door.

II. Diets

I have reported on the diet of the aye-aye in the wild elsewhere (Iwano, 1991a). Here, I focus on the feeding habits of the aye-aye in captivity.

Millot (1952) reviewed studies regarding feeding habits of the aye-aye under human care. The food items the aye-aye has consumed under human care include bananas, mangoes, papayas, datepalms, coconuts, sugar cane, maze, insect larvae, eggs, honey, milk, boiled rice, vegetables, sugar water, grenadine syrup, and cafe au lait. Petter (1977) also confirmed the above.

The basic diet for the aye-ayes now kept in the Paris Zoo consists of coconuts, sugar cane, fruits (mango, avocado, orange, apple, date (*Phoenix* sp. ?), mealworms, protein-rich feed, cheese, and raw eggs; a diet which is practically the same as above (Winn, 1989). The aye-ayes in the Paris Zoo were also given a wide variety of fruits (including fig, pear, etc.), vegetables (carrot, etc.) and nuts (Winn, 1989).

As is evident from above, the aye-aye in captivity can eat a wide variety of plants as well as animal-derived foods such as insects and bee honey. They show some in-

dividual variation in preference to such foods (or more accurately, are influenced by the feeding condition). Moreover, as is suggested from the result of my observations, the aye-aye appears to select the appropriate menu for the season.

Winn (1989) reported that the aye-ayes in the Paris Zoo do not eat tomatoes, but the aye-aye reported here ate tomatoes avidly. Shaw (1883) observed that the aye-aye did not eat honey or egg. This observation is contrary to the results of my study as well as studies of others. According to Lamberton's observation (1934), some aye-ayes like sugar cane while others do not. My aye-aye avidly ate sugar cane from July to September, but rarely ate it from October to November. Such within-species dietary variation among local populations occurs widely in other nonhuman primates (see review by Nishida, 1987).

III. Hard-Nut Adaptation Hypothesis of the Aye-Aye (Iwano & Iwakawa, 1988)

Winn (1989: 114) supported our hypothesis (Iwano & Iwakawa, 1988) based on the observation of an aye-aye's singular feeding behavior in which the aye-aye gnawed open the hard nut (stone) of a fruit, such as a peach, to eat its content.

Furthermore, taking a similar standpoint, she suggested that the feeding of the aye-aye on badamier nuts reported by Petter et al. (1977) could be better explained by consumption of their contents rather than searching for insect larvae hidden within the nuts. The belief that the aye-aye prefers insect larvae is so widespread that Petter et al. (1977) might have been subject to an interpretational bias. In the same way, feeding on the inside of the *Afzelia bijuga* bark at the Nosy Mangabe coast had been interpreted as a search for small living creatures inhabiting the bark (Pollock et al., 1985).

In corroboration of Winn's observation (1989), feeding on fruit stones was also confirmed for the aye-aye at the Tsimbazaza Zoo. After December, Mr. G. Rakotoarisoa gave plums to the aye-aye, which ate the endocarp as well as the mesocarp of the stone. The aye-aye apparently preferred endocarp to mesocarp, and tore open the stone by gnawing and dug out its contents with the third digits.

IV. Energy Intake

The aye-aye's average energy intake per meal is 306 kcal. If the body weight of the aye-aye is assumed to be 2,695 g (based on data presented by Winn, 1989), the energy intake per 100 g for a week corresponds to 79.5 kcal. The same kind of data has been presented by Petter-Rousseaux (1980) for various prosimian species. Comparison of these data reveals that the aye-aye's energy intake is close to that of *Lepilemur ruficaudatus* and substantially different from that of smaller prosimian groups (Table 6).

The proportion of feeding averaged about 14% of the total activity, equivalent to about 89 minutes in terms of total duration spent for feeding. The result is the same whether calculated from the duration of the total activity being 10.6 hours, or from 176.9 sample lengths, the average duration per night in which feeding was recorded. The value lies within the upper limit of continuous stretches of feeding activity on ramy observed in the wild. If the aye-aye spent the same time on

Table 6. Comparison of body weight and energy intake for six Malagasy prosimians species.

Species	Weight g	Energy intake kcal/100g/7day	Reference
Microcebus murinus	65	115	Petter-Rousseaux, 1980
M. coquereli	300	140	Petter-Rousseaux, 1980
Cheirogaleus medius	200	86	Petter-Rousseaux, 1980
Phaner furcifer	300	99	Petter-Rousseaux, 1980
Lepilemur ruficaudatus	500 −900	71	Petter-Rousseaux, 1980
Daubentonia madagascariensis	2,695 —	— 80	Winn, 1989 Present study

feeding on ramy at the rate observed in the wild, it would consume 48.5 ramy fruits or ingest 212 kcal in terms of energy. In contrast, the captive aye-aye's average energy intake per meal, as revealed in the present study, was 306 kcal. This figure is apparently higher than my estimation.

The higher energy intake of the captive animal over its wild counterpart may be due to either of the following two factors: (1) overestimation of the energy intake of the captive animal (a portion of food may only have been torn and thrown away, and not consumed); and (2) increased feeding efficiency under human care in the zoo, allowing the aye-aye to consume a larger quantity of foods in the same interval, thus resulting in increased energy intake. Since zoo food is supplied in far more concentration than in the wild, the latter possibility would be a more important factor in energy intake.

The aye-aye's energy intake value, when presented as energy intake per meal, is not so much different from that of other prosimians, when allowance is made for difference in weight. Thus, the aye-aye in the wild may also ingest a comparable amount of energy with a similar commitment to feeding relative to total activity.

In macaques, the basal metabolic rate (BMR) is believed to be 49 kcal per 1kg weight (Benedict, 1938 quoted from Kleibr, 1975), and BMR for prosimians has been thought to be slightly less (Müller, 1985). Applying the macaque's BMR to the aye-aye, gives 147 kcal as the BMR of an aye-aye weighing 3 kg. Thus, even 199 kcal, or the lowest energy intake ever observed in my aye-aye, would be sufficient to sustain the routine activity of the aye-aye.

V. Response of the Aye-Aye to Light

The response of the aye-aye to light is markedly different from other nocturnal prosimians. The aye-aye was not apparently disturbed when exposed to two intense lights of 150 thousand lux each (brighter than a car's head lights) at a distance of about 2 m, not to mention the light of a torch. This holds true also for aye-ayes in the wild. Whereas other nocturnal prosimians become motionless when exposed to an intense light, aye-ayes, though sometimes watchful of light and human presence, are not apparently disturbed by light.

This characteristic unresponsiveness of the aye-aye to light is quite noteworthy as a trait of a nocturnal animal (it is well known that even a diurnal animal strongly responds to intense light), and should be noted as an unusual characteristic in the behavioral aspects or physiological responsiveness of this animal.

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REFERENCES

Albignac, R. 1986. Status of the aye-aye in Madagascar. In (I. D. Constable, R. A. Mittermeier & S. D. Nash, eds.) *Primates and the Tropical Forest*, pp.44–45, The L. S. B. Leakey Foundation, World Wildlife Fund-U.S., Washington.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 47: 227–267.

Bartlett, A. D. 1862. Observation on the living aye-aye in the Zoological Garden. *Proceedings of the Zoological Society of London*, p.231.

Benedict, F. G. 1938. Vital energetics : a study in comparative basal metabolism. *Carnegie Institution of Washington, Supplementary Publications*, 503: 133,136,149,158,164 (Cited in Kleiber, 1975).

Donque, G. 1972. The climatology of Madagascar. In (R. Battistini & G. Richard-Vindard, eds.) *Biogeography and Ecology in Madagascar*, pp.87–144, Junk, The Hague.

——— & M. Petit 1967. Geographie 3e Madagascar. Hatier, Paris.

Iwano, T. 1991a. An ecological and behavioral study of the aye-aye (*Daubentonia madagascariensis*). *African Study Monographs*, 12(1): 19–42.

——— 1991b. The usage of the digits of the aye-aye (*Daubentonia madagascariensis*). *African Study Monographs*, 12(2): 87–98.

——— & C. Iwakawa 1988. Feeding behavior of the aye-aye (*Daubentonia madagascariensis*) on nuts of ramy (*Canarium madagascariense*). *Folia Primatologica*, 50(1–2): 136–142.

Kleiber, M. 1975. *The Fire of Life—An Introduction to Animal Energetics*, (2nd ed.). Robert E. Krieger Publishing Co., New York.

Lamberton, C. 1934. Contribution à la connaissance de la faune subfossile de Madagascar. *Mém. Acad. Malgache*, 17: 40–46.

Millot, J. 1952. Notes biologiques sur les Lémuriens malgaches. *Le Naturaliste Malgache*, 4(2): 109–121.

Müller, E. F. 1985. Basal metabolic rates in primates—the possible role of phylogenetic and ecological factors. *Comparative Biochemistry and Physiology*, 81A: 707–711.

Nishida, T. 1987. Local traditions and cultural transmission. In (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, eds.) *Primate Societies*, pp.462–474, The Univ. Chicago Press, Chicago.

Owen, R. 1863. On the aye-aye (*Chiromys* Cuvier). *Transactions of the Zoological Society of London*, 5: 33–101.

Petter, J.-J. 1962. Recherches sur l'écologie et l'éthologie des lémuriens malgaches. *Mémories du Muséum National d'Histoire Naturelle*, 27: 1–146.

——— 1977. The aye-aye. In (Prince Rainier III of Monaco & G. H. Bourne, eds.) *Primate Conservation*, pp.37–57. Academic Press, New York.

——— & A. Petter-Rousseaux 1959. Contribution à l'étude du aye-aye. *Le Naturaliste Malgache*, 11(1–2): 153–164.

———, R. Albignac & Y. Rumpler 1977. *Faune de Madagascar 44: Mammifères Lémuriens (Primates Prosimiens)*. ORSTOM CNRS, Paris.

Petter-Rousseaux, A. 1980. Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, in simulated light and climatic conditions. In (P. Charles-Dominique, H. M. Cooper, A. Hladik, C. M. Hladik, E. Pages, G. F. Pariente, A. Petter-Rousseaux, A. Schilling & J. J. Petter, eds.) *Nocturnal Malagasy Primates*, pp.137–167, Academic Press, New York.

Pollock, J. I., I. D. Constable, R. A. Mittermeier, J. Ratsirarson & H. Simons 1985. A note on the diet and feeding behavior of the aye-aye *Daubentonia madagascariensis*. *International Journal of Primatology*, 6(4): 435–447.

Shaw, Rev. G. A. 1883. A few rough notes on the aye-aye. *Proceedings of the Zoological Society of London*, pp.44–45.

Winn, R. M. 1989. The aye-aye, *Daubentonia madagascariensis*, at the Paris Zoological Garden: maintenance and preliminary behavior observations. *Folia Primatologica*, 52: 109–123.

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Author's Name and Address: Taizo IWANO, *Department of Zoology, Faculty of Science, Kyoto University, Kitashirakawa-Oiwake-cho, Sakyo-ku, Kyoto 606, Japan.*